Population position along the fast-slow life-history continuum predicts intraspecific variation in actuarial senescence

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HC and BRS conceived the research questions. HC carried out the capture-recapture analyses and drafted the manuscript. JFL and BRS contributed to writing the manuscript. EB and JP collected field data. All authors gave final approval for publication.

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The data will be available on Dryad after paper acceptance.

Introduction

Most commonly accepted evolutionary theories of ageing posit that survival should decline with increasing age in any age-structured population (Hamilton 1966), a demographic process known as actuarial senescence. Medawar's (1952) mutation accumulation theory first stated that organisms age because the strength of natural selection weakens with age after first reproduction and therefore there is no purging of deleterious mutations that are only expressed late in life. In addition, actuarial senescence can emerge as a by-product of natural selection through antagonistic pleiotropy (Williams 1957). An allele may confer a benefit to the bearer early in life but may also be responsible for an impaired survival later in life. Finally, the disposable soma theory of aging postulates that actuarial senescence can result from a trade-off between allocation to reproduction in early life and somatic maintenance (Kirkwood 1977, Kirkwood & Austad 2000). In other words, individuals that preferentially allocate resources to growth and/or reproduction (e.g., gamete production and parental care) will have much less resources for somatic maintenance (e.g., enzyme-based repair mechanisms), which will ultimately lead to a decline in performance of fitness-related traits (e.g., survival) at advanced ages. So far, most studies focused on aging in the wild have been embedded within the two theoretical frameworks offered by both antagonistic pleiotropy and disposable soma theories of aging as these two theories share the similar prediction of a trade-off between reproductive effort and actuarial senescence (Gaillard & Lemaître 2017).

Although a few case studies on free-ranging populations failed to detect any increase in mortality rate with age (Jones et al. 2014, Cayuela et al. 2019c), most recent syntheses revealed two major facts. First, actuarial senescence is a nearly ubiquitous process in the living world (Nussey et al. 2013, Shefferson et al. 2017). Second, patterns of senescence can be highly variable among species (Jones et al. 2014, Tidière et al. 2016, Colchero et al. 2019). Comparative analyses have shown that senescence patterns across multi-cellular organisms can be predicted by ecological traits, lifestyles and covariation among life-history traits (Péron et al. 2010, Ricklefs 2010, Gaillard et al. 2016, Salguero-Gómez & Jones 2017). In particular, both age at the onset of senescence and rates of senescence appear to be linked to the position of a species along the fast-slow life-history continuum. Organisms that occupy the fast end of the continuum – short generation time, high annual fecundity, and low mean survival rates (Stearns 1983) – tend to experience earlier and faster actuarial senescence than organisms at the slow end of the continuum (Jones et al. 2008a, Salguero-Gómez & Jones 2017). Since life history variation does not only occur among, but also within species (Berven & Gill 1983, Cayuela et al. 2017), intraspecific variation in senescence patterns is expected and can be selected for (Stearns 2000, Stearns et al. 2000, Brommer et al. 2007, Holand

senescence and the speed and the shape of the relationship between mortality rate and age) differed between populations with slow and fast life histories. We focused our analyses on post-metamorphic survival as we did not expect senescence during larval development and assumed that senescence can begin once structural development is completed (i.e., metamorphosis). We expected that the pattern of intraspecific variation in actuarial senescence among populations would be similar to pattern in variation among species. Therefore, we tested the prediction that a fast pace-of-life should be associated with an earlier, faster actuarial senescence among populations of *B. variegata*.

Material and methods

Study system

Bombina variegata populations occur in different types of habitats where the spatiotemporal pattern of breeding resource availability differs widely. In riverine environments, the patches of rock pools used by toads to reproduce are constantly available in space and time, making breeding resources highly predictable at the scale of the lifetime of an individual. By contrast, rut patches resulting from logging operations appear and disappear stochastically in forests, making breeding resource availability unpredictable. The annual probability of patch appearance varies from 0.20 to 0.50 while the rate disappearance ranges from 0.05 to 0.20, depending on the year and the population (Cayuela et al. 2016a).

Previous studies showed that the populations from these two types of environment have different life history strategies. Fast populations from forest environment have accelerated life histories, with lower postmetamorphic survival and higher fecundity than in riverine habitats. Moreover, the fast life history is associated with higher dispersal (i.e., dispersal syndrome) caused by the high patch turn-over resulting from logging operations (Cayuela et al. 2016c, 2019b). Dispersal is facilitated by a phenotypic specialization that is transgenerationally transmitted: individuals from fast forest populations reared in common garden have a higher boldness and exploration propensity than those from riverine slow populations (Cayuela et al. 2019b). The association between high dispersal maintained throughout lifespan, pre-natally determined behavior, and accelerated life history (i.e., life history syndrome; Réale et al. 2010) is likely determined by polygenic bases and gene with pleiotropic effects (Saastamoinen et al. 2018). Furthermore, changes in dispersal regime within spatially structured populations of *B. variegata* lead to strong variation in neutral genetic structure. Fast forest populations have a higher genetic

pattern used to identify individuals is not fixed before that age. Yet, this method permits to survey the toads for the rest of their lives in a non-invasive way. Only individuals can be aged which are one or two years old at first capture (Cayuela et al. 2016b), leading to partially known birth date; this incomplete knowledge of age of individuals is handled using Bayesian survival trajectory analyses (see the section *Capture-recapture modeling*). Sex cannot be assessed with certainty before sexual maturity (2-3 years old) due to the lack of nuptial pads in immature males. For this reason, we did not include an effect of sex in the analyses. Yet, we expect that excluding sex from our analyses should not alter our conclusions since previous studies in these populations did not detect sex-specific effects on survival (Cayuela et al. 2016a, 2016c). Details about the number of survey years, individual age and sampling effort are provided in Appendix 1 (Table 2). A more complete description about the capture-recapture survey, the individual recognition method and population description can be found in Cayuela et al. (2016a, 2016c).

Capture-recapture modeling

We investigated actuarial senescence patterns using Bayesian survival trajectory analyses implemented in the R package BaSTA (Colchero et al. 2012a, 2012b). BaSTA allowed us to account for imperfect detection, left-truncated (i.e., unknown birth date (age)) and right-censored (i.e., unknown death date) capture-recapture data in our analysis. Our analyses focus on the post-metamorphic stage at which senescence is expected to occur (as in Colchero et al. 2019). BaSTA allows estimation of two parameters: age-dependent survival and the proportion of individuals dying at a given age (i.e. age-dependent mortality rate). Given the results of previous analyses (Cayuela et al. 2016a, 2016b), we allowed recapture probabilities to vary among years. As the study period and number of survey years differ among populations (Appendix 1), the four populations were analyzed separately. We used deviance information criterion (DIC) to select models that fitted the data best (Colchero et al. 2019) and we compared the outputs of the best-supported model of the four populations by inspecting mean estimates and 95% credible intervals (CRI) (Anderson et al. 2001, Amrhein et al. 2019). This allowed us to investigate population-specific variation in the shape of the age-specific mortality patterns. We considered the four mortality functions implemented in BaSTA: exponential, Gompertz, Weibull and logistic. For the three last functions, we considered three potential shapes: *simple* that only uses the basic functions described above; *Makeham* (Pletcher 1999); and *bathtub* (Silver 1979). As individuals which are less than one year old cannot be individually recognized, we conditioned the analyses at a minimum age of one. Four MCMC chains were run with 50000 iterations and a burn-in of 5000. Chains were thinned by a

after individuals are 2-3 years old and reached an asymptote at an age of 3 to 4 years. This suggests an early, fast senescence with a short reproductive lifespan.

Age-dependent survival patterns were relatively similar between the populations with the same life history strategies but differed markedly between strategies (Fig. 3). In slow populations (Fig. 3A and 3B), the cumulative probability of surviving until a given age decreased slowly over a toad's lifetime: it was 0.78 until age three, 0.43 until age six, 0.17 until age nine, and finally 0.00 until age 12 (Appendix 1, Table 2-3). In fast populations (Fig. 3C and 3D), cumulative survival probability decreased rapidly after two years: it was 0.58 until age three, 0.07 until age six, and 0.00 until age nine (Appendix 1, Table 4-5).

Discussion

We provide the first clear evidence for actuarial senescence in a wild amphibian that is associated with an intraspecific slow-fast life history difference. The onset of actuarial senescence was earlier in individuals from fast populations and individuals show a faster rate of actuarial senescence than individuals in slow populations.

Population viability, elasticity of demographic parameters, and potential confounding factors

Population matrix models showed that the four populations had population growth rates higher than 1 and can therefore be considered to be viable. Moreover, we highlighted changes in the elasticity of demographic rates: slow population have higher elasticities for adult survival and lower elasticities for pre-breeding survival and fecundity than fast populations. Taken together, our results suggest that life history acceleration in forest populations is not caused by an ongoing demographic decline or transient dynamics. By contrast, variation in life history speed seems to rely on stable demographic strategies covarying with behavioral syndromes that likely have genetic bases (Cayuela et al. 2019b).

Although the habitat type (forest vs riverine) is confounded with latitude in our study system, it is unlikely that the difference in latitude has an effect on demographic traits and actuarial senescence. First, a previous study showed that climate has idiosyncratic effects on population dynamics and there was no evidence for an influence of latitude on demographic rates in *B. variegata* (Cayuela et al. 2016b). Second, populations with slow life history strategies occurring in quarry habitats can be found in the northern part of the study area (Cayuela et al. 2019a), which suggests that latitude is not an important predictor of demographic rates. Third, life history variation

precise quantification of this onset) and had a faster rate of actuarial senescence than individuals from slow populations.

In our study system, individuals from fast populations occurring in forest environment face higher level of environmentally-driven mortality (associated with the unpredictability of breeding patches) than individuals from the slow populations. In fast *B. variegata* populations, logging management frequently lead to the destruction of breeding patches, which decreases adult survival via direct mortality during harvesting operations (Cayuela et al. 2018). In addition, as the natural silting of ruts decreases local breeding success over time, individuals frequently disperse to colonize new patches and likely incur energy and mortality costs related to the different stages of the dispersal process (i.e., emigration, transience, and immigration; Boualit et al. 2019, Cayuela et al. 2019b). By contrast, slow populations occur in non-managed habitats with very limited human activity where dispersal is virtually absent, which likely decrease environmentally-driven mortality (Cayuela et al. 2019b). Since Williams (1957) pioneering contribution on this topic, the relationship between environmentally-driven mortality and actuarial senescence has been heavily discussed (see Gaillard & Lemaître 2017 and Ronget et al. 2017 for reviews). According to Williams (1957), high level of adult mortality should lead to a much stronger rate of actuarial senescence, a prediction which was validated by simulations (Gaillard & Lemaître 2017), at least in absence of density-dependent or condition-dependent mortality over the entire life course (Abrams 1993, Williams & Day 2003; see also Moorad et al. 2019 for a recent review). For instance, if mortality during the juvenile period is strongly condition-dependent, only the most robust individuals will reach adulthood which can postpone and/or decrease actuarial senescence rates (Ronget et al. 2017). Such information is currently lacking in *B. variegata* but would provide important insights on how environmentally-driven mortality modulate the selective forces acting against actuarial senescence.

In our study system, actuarial senescence likely evolves from an adjustment of resource allocation strategies in response to environmentally-driven mortality (Kirkwood & Rose 1991; Stearns 2000, Baudisch & Vaupel 2012). In others words, individuals from the fast populations might be able to cope with higher level of environmentally-driven mortality by allocating more resources to reproduction at the expense of somatic maintenance (see Cayuela et al. 2016a, 2016b for an in-depth discussion). This might ultimately lead to a faster decline in survival probabilities of individuals with age, as expected under the disposable soma theory of ageing (Kirkwood & Austad 2000). In contrast, environmentally-driven mortality is lower in riverine environment where the predictability of breeding patches is high and human activity is virtually inexistent. Accordingly, individuals may allocate fewer resources to reproduction – females produce a lower number of juveniles per year (Cayuela et al. 2016a) – and more to somatic maintenance, resulting

2017), then phylogenetic constraints would be a weak explanation for senescence patterns across the tree of life (Antonovics & van Tienderen 1991). Second, if there is intraspecific variation in senescence, this variation could explain the weakness of the phylogenetic signals in actuarial senescence patterns in several taxa (Salguero-Gómez & Jones 2017). It may well be that phylogenetic signals could become more apparent once intraspecific variation is taken into account. Such a combination of microevolutionary and macroevolutionary patterns of senescence would lead to a deeper understanding of the evolutionary biology of senescence.

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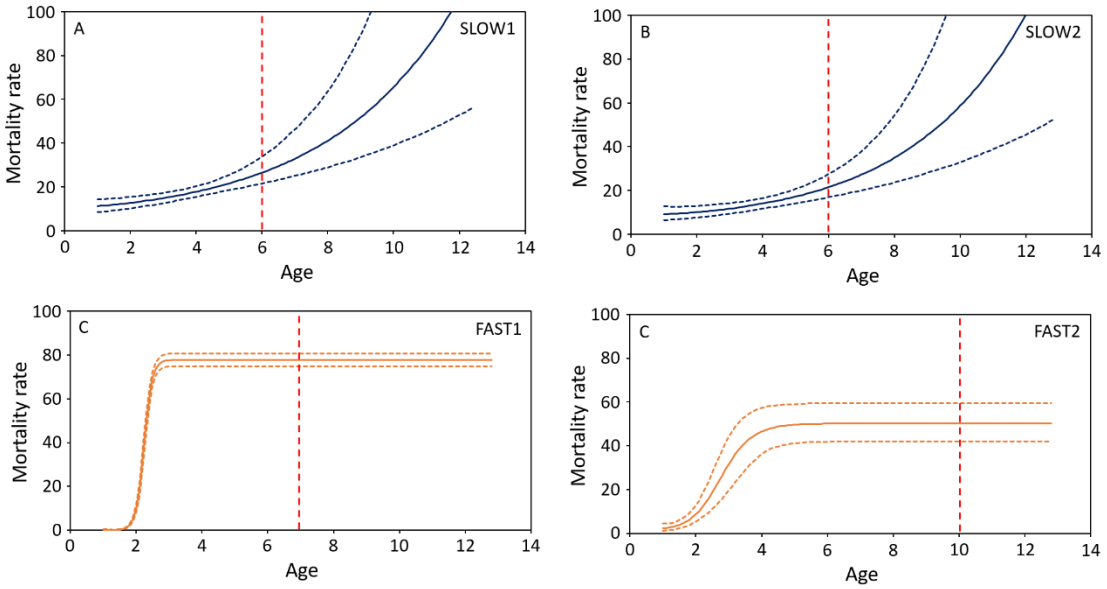
611

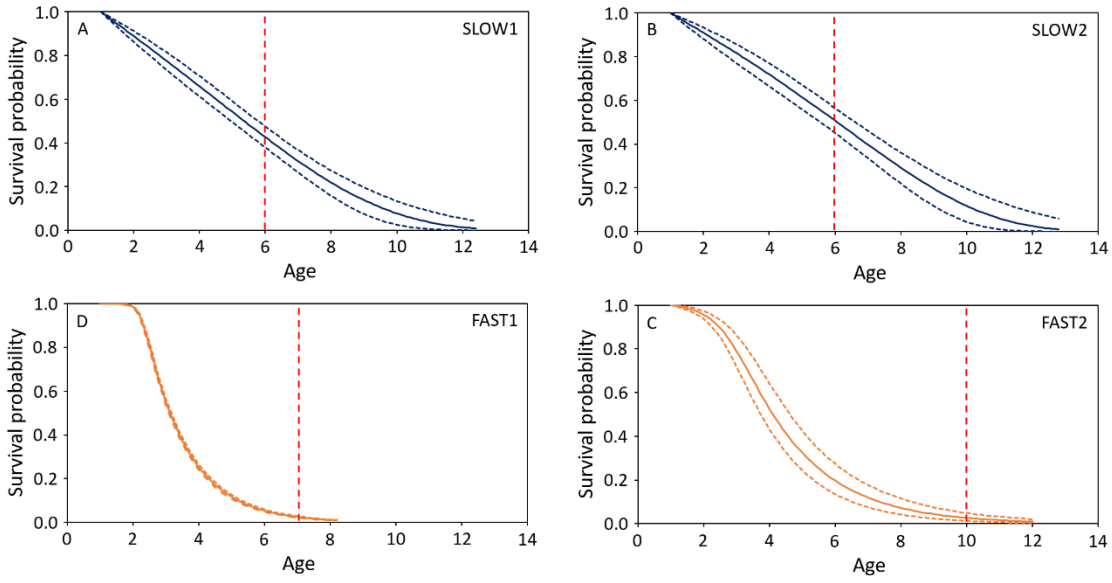
Table 2. Model selection results. Deviance information criterion (DIC) for each of the mortality function considered in the four studied populations of *Bombina variegata*. We considered the four mortality functions implemented in BaSTA program: exponential (EXP), Gompertz (GOM), Weibull (WEI) and logistic (LOG). For the three last functions, we considered three potential shapes: simple that only uses the basic functions described above ("simple"); Makeham ("make"); and bathtub ("bath").

Function	SLOW1	SLOW2	FAST1	FAST2
LOG_simple	13883.1	9770.011	6539.856	79770.16
LOG_bath	13408.63	9511.085	**6164.568**	**76039.06**
LOG_make	13878.78	9706.06	6559.085	79669.19
EXP	16151.69	11085.02	8179.035	120984.4
GOM_simple	13515.9	9104.43	6859.955	91054.45
GOM_bath	**13210.67**	**8855.467**	6797.639	89020.97
GOM_make	13534.36	9065.034	6888.318	91053.47
WEI_simple	13793.82	9451.142	6811.184	87726.47
WEI_bath	13406.18	9230.966	6653.47	85057.55
WEI_make	13790.13	9464.459	6805.522	87757.15



631

632 **Fig. 2.** Mortality rate (i.e., proportion of individuals dying at a given age) in two fast (FAST1 and
633 FAST2) and slow (SLOW1 and SLOW2) populations of *Bombina variegata*. The predictions on
634 the left of the vertical dashed line correspond to observed ages while those on the right are model
635 projections.



636

637 **Fig. 3.** Survival probability until a given age in two fast (FAST1 and FAST2) and slow (SLOW1
638 and SLOW2) populations of *Bombina variegata*. The predictions on the left of the vertical dashed
639 line correspond to observed ages while those on the right are model projections.

640